Microclimate affects the distribution of grassland birds, but not forest birds, in an Alpine environment

Microclimate Affects the Distribution of Grassland Birds, but not Forest Birds, in an Alpine Environment

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Abstract

Predictions derived from species distribution models (SDMs) are strongly influenced by the spatial scale at which species and environmental data (e.g. climate) are gathered. SDMs of mountain birds usually build on large-scale temperature estimates. However, the topographic complexity of mountain areas could create microclimatic refuges which may alter species distributions at small spatial scales. To assess whether fine-scale data (temperature and/or topography) improve model performance when predicting species occurrence, we collected data on presence-absence of bird species, habitat and fine-scale temperature at survey points along an elevational gradient in the Alps (NW Italy). Large-scale temperature data, and both large- and fine-scale topography data, were extracted from online databases for each point. We compared species models (fine-scale vs large-scale) using an information-theoretic approach. Models including fine-scale temperature estimates performed better than corresponding large-scale models for all open habitat species, whereas most forest/ecotone species showed no difference between the two scales. Grassland birds such as Northern Wheatear *Oenanthe oenanthe* and Water Pipit *Anthus spinoletta* were positively associated with warmer microclimates. These results suggest that alpine grassland species are potentially more resistant to the impact of climate change than previously predicted, but that indirect effects of climate change such as habitat shifts (forest- and shrub encroachment at high elevations) pose a major threat. Therefore, active management of alpine grassland is needed to maintain open areas and to prevent potential habitat loss and fragmentation. SDMs based solely on large-scale temperatures for open habitat species in the Alps should be re-assessed.

Key words: information-theoretic approach, mountains, species distribution models, temperature, topography.

Introduction

Species distribution models (henceforth SDMs) are a widely used tool in conservation (Guisan and Thuiller 2005, Rodríguez et al. 2007, Franklin 2013) for a range of taxa (Ongaro et al. 2018, Lewthwaite et al. 2018, Hof and Allen 2019). In the face of climate change, SDMs have become particularly important in predicting current and/or future distributions of species under different climate change scenarios (Avalos and Herández 2015, Jackson et al. 2015, Lehikoinen and Virkkala 2016). These studies usually rely on macroclimate data, which describe climatic conditions at a relatively large scale (approximately one square kilometre or more; Zellweger et al. 2019) derived from national networks, weather stations or online databases (e.g Worldclim; Hijmans et al. 2005).

However, mountain environments are often poorly represented by conventional climate station data, and uncertainty for interpolated climatic values is high (Hijmans et al. 2005). Furthermore, local temperature can vary substantially due to the topographic complexity in mountain areas (Scherrer and Körner 2010, Gunton et al. 2015), thus creating a mosaic of microclimatic conditions over small spatial scales. Depending on discipline, microclimates have been defined in various ways. In this study, we adopt the definition by Bramer et al. (2018) who defined microclimate as fine-scale climate variations at spatial resolutions of < 100m, which are influenced by fine-resolution biotic and abiotic variations (topography, soil type and vegetation). Topographic variables like aspect and slope can markedly alter microclimate by influencing the amount of incoming solar radiation between different exposed slopes. Between north and south exposed slopes, temperature can differ by approximately 1°C if slopes are gentle (<5°) but can increase up to 5°C if slopes are steep (40°; Gubler et al. 2011). Moreover, these differences could subsequently influence snow accumulation processes and thus the rate of snow melt in spring (Gubler et al. 2011).

There is mounting evidence of the importance of microclimate in influencing habitat selection. For example, Bramblings *Fringilla montifringilla* tend to rest in higher densities in areas with warm microclimatic conditions (Zabala et al. 2012). In Mountain Chickadees *Poecile gambeli*, microclimates influence the selection of foraging sites (Wachob 1996). Microclimates

can also act as thermal refuges, which enable individuals to persist despite unfavourable ambient conditions (Wilson et al. 2015). This has been shown in Northern Bobwhites *Colinus virginianus,* which mitigated thermal stress by seeking thermally-buffered microclimatic sites during hot days (Carroll et al. 2015). Furthermore, Northern Bobwhite nest site selection was proven to be influenced by microclimate: Individuals nested in cooler and moister microclimatic conditions compared to surrounding non-nesting locations (Tomecek et al. 2017, Carroll et al. 2018).

Only a few studies have investigated the role of microclimate within a mountain context. Frey et al. (2016) showed that fine-scale temperature metrics were strong predictors of bird distributions, with temperature effects being larger than vegetation effects on occupancy dynamics in mountain forests (but see Viterbi et al. 2013). In the Alps, the habitat of the alpine Rock Ptarmigan *Lagopus muta helvetica* is characterised by a wide variety of microclimates over small spatial scales with individuals choosing colder sites in summer (Visinoni et al. 2015).

Beside the direct impact on birds, microclimate also plays a crucial role in habitat selection in insects. It has been demonstrated that in *Parnassius apollo,* a mountain specialist butterfly, larval habitat selection is related to ambient temperature. Larvae selected warm microclimates when ambient temperatures fell below a threshold of 27°C, whereas cold microclimates were selected when this threshold was exceeded (Ashton et al. 2009). Microclimate can further influence oviposition (Stuhldreher et al. 2012), and the precise microclimatic conditions for thermoregulation are actively sought by montane species of the genus *Erebia* (Kleckova et al. 2014). In this respect, microclimate won't only shape the distributions of these butterfly species, but it will also indirectly influence bird species which rely on caterpillars as a food source for chick rearing.

Microclimate thus has the potential to influence many aspects of an organism's life cycle. It could help to buffer or to compound the effects of climate change (Spasojevic et al. 2013). To assess the impact of climate change on current or future distributions of species it is crucial to gather climate data at the most appropriate scale in order to increase model accuracy (Barton et al. 2018, Randin et al. 2009). However, predictions for future geographic

distributions of mountain birds under a range of climate change scenarios have thus far been based on models which have considered climate variables measured at large scales, usually ca. 1 km^2 (Chamberlain et al. 2013, 2016, Brambilla et al. 2016, 2017a). Given the potential for bird responses to microclimatic conditions in mountains (Frey et al. 2016, Visioni et al. 2014), it may be more appropriate to consider the role of climate measured at finer spatial resolutions in determining mountain bird distributions. This is particularly important given that environmental conditions in mountains typically change over very small spatial scales thanks to steep elevation gradients (Scherrer and Körner 2010, Gunton et al. 2015).

In this study, we investigated the role of microclimate for a range of Alpine ecotone and open habitat species. There were two specific aims. First, to evaluate if models including a microclimatic variable (in this case temperature) show better performance than models using large-scale climate estimates. This will inform future modelling studies, and should help to improve predictions of future impacts of climate change on Alpine birds where microclimatic effects are evident. Second, to assess if models including topographic variables (slope and aspect) in combination with climatic variables (fine and large scale) increase model performance. This will assess the extent to which topographic variables should be included in SDMs of alpine bird species. Based on previous studies, which showed that microclimate can influence bird distributions within mountain habitats (Frey et al. 2016, Visinoni et al. 2015), we hypothesise that models using fine-scale temperature estimates will show better model performance than models using large-scale temperature estimates.

Methods

Study area and point selection

The study was carried out in Val Troncea Natural Park (44°57’28” N; 6°56’28” E) in the western Italian Alps. At lower elevations, the area is dominated by larch *Larix decidua*. The natural treeline is typically found at around 2200 m asl, but varies depending on local conditions. Typical shrub species are *Juniperus nana* (henceforth Juniper) and *Rhododendron ferrugineum* (henceforth Rhododendron) which rapidly encroached wide areas of grasslands

after the decline of agro-pastoral activities. Grasslands are mainly dominated by *Festuca curvula*, *Carex sempervirens*, and *Trifolium alpinum*. Scree and rocky areas occur predominantly at higher elevations, above approximately 2700 m asl.

Point counts were carried out along an elevational gradient ranging from 1750 m to 2820 m encompassing forest, ecotone and open habitats. Point count locations coincided with the centroids of a pre-existing grid at a scale of approximately 150 x 150 m (there was some variation, due to access constraints for example; Probo et al. 2014) along the western facing slope of the valley. All points were spaced a minimum of 200 m apart.

Bird surveys

Point counts (n = 221) were carried out from mid-May to mid-July 2017 following the methods of Bibby et al. (2000), using a 10 minute count period. At each point count location, all individual birds seen or heard were recorded within a 100 m radius (estimated with the aid of a laser range finder). Point counts commenced 1-1.5 h after sunrise and continued until 1200 h. Surveys did not take place in excessively wet or windy conditions. Each point count location was visited once.

Habitat data collection

At each point count location, habitat data were collected through the visual estimation of the percentage cover of canopy (i.e. vegetation above head height), the dominant shrub species, open grassland and bare rock (including scree and unvegetated areas) within a 100 m radius of the point's centre. The dominant shrub species were defined into four groups: Rhododendron, Juniper, bilberry (*Vaccinium myrtillus and V. gaultherioides)* and other (e.g. Green Alder *Alnus viridis,* Willow *Salix spp,* and also including young trees less than two meters in height, mostly European Larch *Larix decidua*). Furthermore, the number of mature trees (greater than c. 20 cm in diameter at breast height) within a 50 m radius of a point count location was counted. These estimates have been shown to correlate well with estimates of

land cover derived from remote sensing and have been used as the basis of predictive models for several species considered here (Chamberlain et al. 2013, 2016, Jähnig et al. 2018).

Temperature measurements

At each point count location, temperature was measured with hygro buttons (Plug & Track™), using methods based on Frey et al. (2016). Each button was stuck on the bottom of a small plastic cup, which was attached upside down to a bamboo stick to protect the button against wind, direct sunlight and water. Mean button height was 40.89 cm (min = 28 cm, max = 47 cm). Hygro buttons were programmed to record temperature every 5 minutes. They were placed 24 hours before a point count commenced and were collected 24 hours after the point count ended, which resulted in a total recording time of 48 hours. At every hygro button location, button height, distance to slope, substrate and canopy presence/absence was recorded.

Statistical analysis

Temperature modelling

For each point count location, minimum, maximum and mean temperatures were derived over the 48 hour recording period. All temperature measurements were checked for collinearity by calculating Pearson's correlation coefficient. Mean temperature was strongly correlated with both minimum ($r = 0.80$) and maximum temperature ($r = 0.73$) over the recording period. Therefore, temperature modelling was undertaken with mean temperature values. The same procedure was repeated for night-time temperatures. Minimum, maximum and mean night-time temperatures were obtained for the time period between 23.00 pm and 03.00 am over the same recording period at each point. There was a strong positive correlation of mean night-time temperature between minimum ($r = 0.97$) and maximum night-time temperature ($r = 0.89$).

The objective of the first analysis was to model temperature in relation to date and elevation. This model was then used to predict a standardised temperature at each point count

location, set at a fixed date, which was representative of the fine-scale temperature at that point controlling for seasonal effects. This procedure provided data which was analogous to the larger scale temperature data (see below). This standardised temperature was then used subsequently as a variable in species distribution models. Note that all subsequent modelling steps were performed separately for mean temperature and mean night-time temperature. However, models with night-time temperature were very similar to those using mean temperature, so we focus on the latter. Further details on night-time temperature models are given in the Electronic Supplementary Material (ESM) Table S1.

First, to investigate if temperature recording was influenced by characteristics of the hygro button's position, it was analysed using a generalised linear model in relation to button height, distance to slope, substrate underneath the button and canopy presence/absence, specifying a normal error distribution. None of the variables showed a significant effect on mean temperature ($p > 0.05$), therefore they were not considered further in the analysis.

In the next modelling step, standardised temperature estimates were derived separately for open Alpine grassland and forest/ecotone habitat, i.e. models were used to estimate temperature for a given elevation whilst accounting for seasonal variation. Points were classified as Alpine grassland if there was no canopy within 100m radius of the point count centre (following Chamberlain et al. 2013). For open habitat points (n = 93), temperature was modelled in relation to date and elevation. Date was described as the number of days passed since the start of the field season, where day 1 = 27-May-2017. Canopy cover was added to the model structure for points located in forest and ecotone habitat (n = 128). In both cases, a normal distribution was specified. Prior to modelling, all variables were scaled and centred using the scale function in R. Collinearity was assessed using Variance inflation factors (VIFs), calculated using the 'corvif' function (package 'AED', Zuur et al. 2009), and by considering Spearman correlations between continuous variables. All variables had VIF < 3, and no pair of variables showed a correlation > 0.7, indicating low levels of inter-correlation. These models were used to derive a standardised temperature for each point, based on the elevation at that point, the canopy cover (for forest/ecotone habitat) and for a date fixed at 15th June.

222

223 *Species distribution models*

224 Birds detected within a 100-m radius of a point count location were used to analyse species
225 distribution (presence/absence of individual species). Bird species were considered in the
226 modelling process if they were present on at least 15 % of the points; below this threshold
227 model performance is consistently poor (Chamberlain et al. 2013).

228 The commonest species were modelled in relation to four different variable sets: (i) habitat
229 (HABITAT), (ii) habitat + temperature (TEMP), (iii) habitat + topography (TOPO), (iv) habitat +
230 temperature + topography (COMB; Table 2). Temperature and topographic variables were
231 used at two different scales (large-scale/ fine-scale). Fine-scale temperature estimates were
232 derived from the temperature modelling approach described above, whereas large-scale
233 temperature data for each point were extracted from the Worldclim database (Hijmans et al.
234 2005) by calculating the average temperature within a 1000 m radius of the point count centre.
235 Topographic variables (aspect and slope) were derived from a Digital Elevation Model (DEM)
236 at a spatial resolution of 10 metres. Aspect was transformed as $x = -1*\cos[Ø(\pi/180)]$, where Ø
237 is measured in degrees. Values ranged from 1 where solar insolation was higher (south-facing
238 slopes) to -1 (north-facing slopes) where it was lower.

239 The mean aspect (transformed values) and slope was calculated within a 100 m (fine-
240 scale) and a 1000 m (large-scale) radius of the point count centre for the analysis. Habitat
241 variables were kept at a constant scale in the models (as the objective was to test scale effects
242 in temperature and topography).

243 Habitat models of Lesser Whitethroat *Sylvia curruca* and Dunnock *Prunella modularis*
244 were tested for non-linear relationships with Rhododendron and Juniper cover as suggested
245 by previous work(Jähnig et al. 2018). Habitat models with and without quadratic terms for shrub
246 species cover were compared using AIC. Lesser Whitethroat models showed lower AIC values
247 for the habitat model without quadratic terms. Therefore these were omitted in further modelling
248 steps. The addition of the quadratic term for Rhododendron cover reduced the AIC of the
249 habitat model for Dunnock by $\Delta AIC > 2$, hence it was included in the next modelling steps.

The occurrence probability of each species was modelled in relation to the different variable sets using a binomial logistic regression, after controlling for potential collinearity (as above). In the case of open habitat species, we found high VIFs for the variables rock and grass cover. After the removal of rock cover, all VIFs were below the threshold of three. As a result, rock cover was removed from all models for open habitat species.

Data were analysed using an information theoretic approach with the MuMIn package in R version 3.5.2; (R Development Core Team 2018, Bartón 2013). This entailed deriving full models for each variable set at each scale (except habitat which was kept constant in all models) using generalised linear models (R package lme4; Bates et al. 2015). This approach served two goals. First, model-averaged parameter estimates were derived for all combinations of variables in each full model set in order to identify variables that were most closely associated with bird distribution. *p*-values derived from the model-averaged parameter estimates and their SEs were considered to represent significant effects when $p < 0.05$. Second, the Akaike information criterion corrected for small sample size (AICc) was determined for each individual model and was used to assess model performance for different variable combinations at different scales in the full model. In this way it was possible to assess which combination of the four different variable sets produced the best models, and at which scale.

At each scale, the residuals for all full models were extracted and tested for spatial autocorrelation using Moran's *I* (Moran 1950). Significant spatial autocorrelation was found for models of Eurasian Skylark *Alauda arvensis*, Tree Pipit *Anthus trivialis* and Water Pipit. For these species, spatial effects were incorporated by modelling their distributions using Generalized Additive Models (GAMs) from the mgcv package (Wood 2011) by fitting smoothed terms for latitude and longitude in the model, following Wood (2017).

Results

In total, 862 individuals of 40 species were recorded in 221 point counts over an elevational range of 1750 – 2800 m a.s.l. There were seven species that were recorderd on at least 15%

of the points within forest and ecotone habitat: Dunnock, Lesser Whitethroat, Chaffinch *Fringilla coelebs,* Mistle Thrush *Turdus viscivorus,* Coal Tit *Parus ater,* rock bunting *Emberiza cia,* Tree Pipit and three species within open habitat: Eurasian Skylark, Water Pipit and Northern Wheatear.

The best model to predict rock bunting occurrence was always the null model for each model set at each scale, with no model-averaged parameter estimates being significant. Therefore, this species was not considered further in the analysis.

Forest and ecotone species

Habitat variables such as trees and shrubs were the variables most commonly associated with species occurrence within the HABITAT model for forest and ecotone species. In general, the results of the HABITAT models were in line with previous findings by Jähnig et al. (2018). Juniper showed a positive relationship with Coal Tit, Dunnock and Lesser Whitethroat, but was negatively related to Tree Pipit presence. Rhododendron was positively associated with Mistle Thrush and Lesser Whitethroat presence, whereas it showed a non-linear relationship with Dunnock presence. The number of mature trees showed a positive relationship with forest species (Chaffinch, Mistle Thrush and Coal Tit). Habitat associations among the species remained mostly constant in TEMP, TOPO and COMB models (for full details see ESM Table S2, S4).

Each variable set at each scale performed equally well for Lesser Whitethroat, Mistle Thrush and Coal Tit (Table 3). (Note that full details of all models are given in ESM Table S3). Large-scale temperature and topographic variables were included in the best performing model for Dunnock, temperature being negatively associated with Dunnock presence (Table 4, Fig. 1). In contrast, large-scale temperature showed a positive relationship with Chaffinch presence in models including only large-scale temperature (Table 4, Fig. 1), or in models including a combination of large-scale temperature and topographic variables. In both species, large-scale model sets performed better than their fine-scale equivalents. Large-scale models for TOPO and COMB were the best performing models for Tree Pipit, whose presence was

more closely associated with large-scale topographic variables such as aspect, for which it showed a strong negative relationship indicating a preference for westerly over southerly slopes (Fig. 2). Beside Tree Pipit, only Mistle Thrush showed a negative association with aspect. No other species showed any association with slope or aspect. Furthermore, Tree Pipit was the only species that showed better model performance (ΔAICc ≤ 2) for the large-scale TOPO model compared to all fine-scale models and the large-scale TEMP model. All other species showed better (Chaffinch) or equal model performance of TEMP models compared to TOPO models at both scales.

Open habitat species

The HABITAT model for each open species did not show any habitat associations among the recorded variables. However, all fine-scale models (TEMP, TOPO and COMB) showed a positive association between grass cover and Skylark presence while Juniper cover was only positively associated in the TEMP and COMP models.

Models including fine-scale temperature and topography performed best (ΔAICc ≤ 2) for Northern Wheatear. The best performing models of Skylark and Water Pipit included both fine-scale TEMP and COMB models. Fine-scale temperature was positively associated with Water Pipit and Northern Wheatear presence, whereas Eurasian Skylark presence was negatively associated (Table 4, Fig. 3).

At a fine scale, TEMP models showed better model performance than TOPO models for Northern Wheatear and Water Pipit, whereas on a large scale, model sets for TEMP and TOPO were overlapping (Northern Wheatear, Water Pipit). The large-scale TOPO model showed equal model performance compared to the large-scale TEMP model for Skylark, but AIC_c was still higher compared to fine-scale COMB. In addition, aspect showed a positive relationship with Northern Wheatear (Fig.2, fine-scale COMB model) and Skylark presence (large-scale TOPO model) while slope was positively related to Skylark presence in the fine-scale TOPO model.

Discussion

Models including fine-scale temperature estimates (TEMP, COMB) showed better model performance ($\Delta AIC_c < 2$) than corresponding large-scale models for all three open habitat species. Northern Wheatear and Water Pipit were both positively associated with warm microclimates while Skylark presence was negatively associated with fine-scale temperature. These results contrast with previous findings from the same region of the Alps (Chamberlain et al. 2013, 2016), where model predictions were based on large-scale climatic variables. In these studies, SDMs (based on temperature change and assuming no change in habitat) suggested that under warmer conditions, Skylark and Northern Wheatear would show an increase in their distribution whereas Water Pipit distribution would decrease. Therefore, for Water Pipit and Skylark distributions, our findings suggest opposite associations between fine-scale and large-scale temperature.

Differences in model predictions at different spatial scales have been reported for a range of studies, and thus identifying the appropriate scale represents a major problem when forecasting suitable habitat in order to inform conservation planning (Elith and Leathwick 2009, Randin et al. 2009, Franklin et al. 2013, Logan et al. 2013, Scridel et al. 2018). To improve SDMs, it is therefore necessary to carefully select predictors (e.g. temperature variables) and their spatial resolution. In the case of microclimate, local topography could create areas with suitable climatic conditions under which it would still be possible for a species to persist under the impact of climate change. Through the use of large-scale climate data, these areas might not be recognised by SDMs (Austin et al. 2011). Besides affecting the future distribution of a species, microclimate can also influence many other aspects of a species' life cycle.

There is evidence that microclimate can be important in influencing habitat selection in mountain birds which may explain our findings. For example, it has been shown that Horned Larks *Eremophila alpestris* adjusted the amount of incubation time in response to microclimatic conditions (Camfield and Martin 2009) by spending less time on the nest as temperatures in the nest surrounding increased, which may imply energy savings in warmer microclimates. Furthermore, microclimate and aspect strongly influenced nestling survival in Water Pipits

(Rauter et al. 2002). Nests which were located at ENE-facing slopes (temperature maximum in the morning) had more fledglings than those on WSW-facing slopes (temperature maximum in the afternoon). In contrast, foraging habitat selection by alpine White-winged Snowfinches *Montifringilla nivalis*, a high altitude specialist, was influenced by solar radiation (Brambilla et al. 2017b). Snowfinches preferred to forage at colder sites (low solar radiation) throughout the season. These studies illustrate that behaviour, foraging habitat selection and choice of nest sites could be driven by microclimatic conditions thereby affecting bird species distributions. Therefore, we would strongly recommend considering microclimate as a predictor in future SDMs for open habitat Alpine species.

In contrast to the open habitat species considered, forest and ecotone species showed no association with fine-scale temperature. One possible reason might be the buffering effect of vegetation. Körner et al. (2007) showed that temperature can vary strongly between forest and open alpine grassland along the elevation gradient with intermediate values at the treeline ecotone. Furthermore, canopies can buffer the diurnal amplitude of air temperature in the forest (Chen et al. 1999).

For two species (Dunnock and Chaffinch) large-scale models including temperature (TEMP, COMB) performed better than fine-scale models. The probability of occurrence of Chaffinch was positively associated with large-scale temperature, whereas the probability of Dunnock presence was negatively affected. A future increase in temperature could therefore affect the distribution of Chaffinches by expanding its range towards higher elevations. In contrast, the distribution of Dunnocks might be severely limited. Bani et al. (2019) demonstrated that Dunnock distribution experienced a lower range contraction along the elevational gradient during the last 35 years, but a simple dispersal into higher elevations as a response to environmental change might not be possible because it's preferred nesting habitat in our study area, Rhododendron, has a slow rate of colonisation to the extent that treeline shifts towards higher elevations are likely to be more rapid than upwards shifts in this species (Komac et al. 2016).

389 The mismatch between temperature and available future habitat can also affect open
390 habitat species considered in this study. Due to increasing temperatures, shifts in major habitat
391 types (i.e. forest and shrub encroachment; Harsch et al. 2009) may lead to habitat
392 fragmentation and/or loss of open alpine grassland at higher elevations. This process might
393 even be exacerbated by the abandonment of pastoral activities which formerly have
394 maintained the forest limit at lower elevations than would be possible under climatic constraints
395 only (Gehrig- Fasel et al. 2007).
396
397 Topography
398 For the majority of species, COMB models performed equally well in comparison with TEMP
399 models at both spatial scales. Combining temperature with topographic variables increased
400 model performance only for Northern Wheatear and Skylark at a fine scale. For the former
401 species, occurrence was more closely related with south-facing slopes. At a large scale, the
402 probability of Tree Pipit presence was higher on westerly slopes. However, in general
403 topographic variables were rarely associated with species occurrence. The influence of aspect
404 on the occurrence of some species could be explained by its effect on snow melt patterns
405 during spring. Thermal differences among slopes with different exposition, which are caused
406 by the amount of received solar radiation, could lead to an early snow melt on south-exposed
407 slopes whereas north-exposed slopes might stay snow covered for a longer period (Keller et
408 al. 2005). These early snow free areas could potentially benefit Northern Wheatears by making
409 suitable nesting sites available earlier. Furthermore, it has been shown that differences in
410 temperature among slopes can influence plant species diversity in temperate mountains
411 (Winkler et al. 2016) with south-exposed slopes favouring a higher degree of species richness
412 and diversity which may in turn influence insect availability.
413
414 Conservation implications
415 Previous studies from the Italian Alps have indicated that increasing temperatures could have
416 detrimental effects for certain Alpine species in the future (Chamberlain et al. 2013), with some

417 species being potentially impacted by both temperature and habitat shifts (Water Pipit), while
418 for others, loss of habitat due to forest and shrub encroachment will likely be more important
419 (Northern Wheatear, Skylark).

420 However, our results have shown that species such as Water Pipit and Northern
421 Wheatear are positively associated with warm microclimates which could indicate that both
422 species are potentially more resistant to the impact of a warming climate than previously
423 emphasised by large-scale temperature modelling (e.g. Chamberlain et al. 2013). As a
424 consequence, our results imply that changes in habitat in the form of advancing treelines and
425 the encroachment of formerly open areas by shrubs and trees (Gehrig-Fasel et al. 2007,
426 Leonelli et al. 2011) are currently the major threat to those Alpine species, rather than direct
427 effects of temperature. Therefore, it becomes particularly important to actively manage open
428 areas within mountain environments. This could be achieved by targeted grazing techniques
429 such as mineral mix supplements (Pittarello et al. 2016) or temporary night camp areas (Tocco
430 et al.2013). Both techniques lead to the mechanical damage of shrubs (including saplings) and
431 eventually result in a reduction of shrub cover (Probo et al. 2013, 2014).

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434

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438

439 **Figure legends**

440

441 **Fig. 1** Relationship between large-scale temperature and the probability of occurrence of
442 Dunnock and Chaffinch based on the large-scale COMB model. Shading indicates the 95%
443 confidence interval.

444

Fig. 2 Relationship between aspect and the probability of occurrence for Tree Pipit and Northern Wheatear for the large-scale TOPO and the fine-scale COMB model, respectively. Note that aspect was modelled as an index from 1 (south-facing) to -1 (north facing), but here we present the axis as the equivalent cardinal direction for ease of interpretation. Shading indicates the 95% confidence interval.

Fig. 3 Relationship between fine-scale temperature and probability of occurrence for open habitat species for the fine-scale COMB model. Shading indicates the 95% confidence interval.

Table 1 Variables considered in the analysis, and the scale at which they were measured.

Parameter	Scale	Description
Canopy	fine	Percentage cover of canopy (above head height) within a radius of 100 m of the point count centre
Rod	fine	Percentage cover of Rhododendron within a radius of 100 m of the point count centre
Jun	fine	Percentage cover of Juniper within a radius of 100 m of the point count centre
Vac	fine	Percentage cover of bilberry within a radius of 100 m of the point count centre
Oth	fine	Percentage cover of shrubs different from Juniper, Rhododendron and bilberry within a radius of 100 m of the point count centre
Grass	fine	Percentage cover of grass within a radius of 100 m of the point count centre
Rock	fine	Percentage cover of rock within a radius of 100 m of the point count centre
Trees	fine	Number of mature (greater than ca. 20 cm in diameter) trees within a radius of 50 m of the point count centre
Temp	fine	Modelled fine-scale standardised average temperature of the point count centre
Temp	large	Large-scale average temperature within 1000 m of the point count centre extracted from WorldClim.
Aspect	fine	The average direction a slope is facing within a 100 m radius of the point count centre transformed as $x= -1*\cos[Ø(\pi/180)]$, where Ø is measured in degrees.
Aspect	large	The average direction a slope is facing within a 1000 m radius of the point count centre transformed as $x= -1*\cos[Ø(\pi/180)]$, where Ø is measured in degrees.
Slope	fine	The average inclination of the surface within a 100 m radius of the point counts centre measured in degrees.
Slope	large	The average inclination of the surface within a 1000 m radius of the point counts centre measured in degrees.

Table 2 Variable combinations for each model set. Model sets for TEMP, TOPO and COMB were considered at two different scales (fine and large) and included temperature, slope and aspect at their matching scale. The variables Rock and Trees were omitted from the habitat model for open habitat species (Northern Wheatear, Water Pipit and Skylark).

Full models	Parameter
HABITAT	Rod + Jun + Vac + Oth + Grass + (Rock) + (Trees)
TEMP	Rod + Jun + Vac + Oth * Grass + (Rock) + (Trees) + Temp
TOPO	Rod + Jun + Vac + Oth * Grass + (Rock) + (Trees) + Slope + Aspect
COMB	Rod + Jun + Vac + Oth * Grass + (Rock) + (Trees) + Temp + Slope + Aspect

Table 3 ΔAIC_c value for each model set at each scale for all species. A ΔAIC_c value of zero indicates the best performing model. Note that in some cases, the best performing models were identical in different model sets, hence a value of zero can appear more than once for a given species. Original AIC_c values are listed in ESM Table S3.

	HABITAT	**TEMP**		**TOPO**		**COMB**	
Species	fine-scale	fine-scale	large-scale	fine-scale	large-scale	fine-scale	large-scale
Prunella modularis	3.9	2.7	0.8	3.9	3.9	2.7	0
Sylvia curruca	0	0	0	0	0	0	0
Parus ater	1.4	1.4	0	1.4	1.4	1.4	0
Turdus viscivorus	1.2	1.2	1.2	0	1.2	0	1.2
Fringilla coelebs	13.9	6.3	0	13.1	12.9	6.3	0
Anthus trivialis	10	8.5	10	9.8	0	8.4	0
Oenanthe oenanthe	7.7	3.5	7.7	5.8	6.5	0	6.5
Anthus spinoletta	4.6	0.9	4.6	3.2	4.6	0	4.6
Alauda arvensis	6.0	0.9	2.7	2.3	4.8	0	2.7

Species	Model	Scale	Parameter	Estimate	SE	*z*	*p*
Prunella modularis	COMB	large	Rod	1.285	0.618	2.068	0.038
			Jun	0.818	0.308	2.632	0.008
			Oth	0.580	0.270	2.126	0.033
			Temp	− 0.886	0.406	2.163	0.030
*Sylvia curruca**	TEMP	fine	Rod	1.029	0.265	3.835	≤ 0.001
			Jun	0.624	0.265	2.332	0.019
			Rock	− 1.174	0.467	2.487	0.012
*Parus ater**	COMB	large	Jun	0.677	0.333	2.017	0.043
			Oth	0.657	0.277	2.351	0.018
			Grass	0.938	0.434	2.145	0.031
			Trees	1.126	0.303	3.678	≤ 0.001
*Turdus viscivorus**	TOPO	fine	Vac	− 1.700	0.823	2.049	0.040
			Aspect	− 0.644	0.316	2.017	0.043

Fringilla coelebs	TEMP	large	Trees	2.453	0.809	3.004	0.002
			Temp	1.500	0.462	3.218	0.001
Anthus trivialis	TOPO	large	Jun	− 1.187	0.399	2.939	0.003
			Aspect	− 2.614	0.644	4.022	≤ 0.001
Oenanthe oenanthe	COMB	fine	Temp	0.736	0.305	2.386	0.017
			Aspect	0.622	0.288	2.133	0.032
Anthus spinoletta	COMB	fine	Temp	1.336	0.577	2.281	0.022
Alauda arvensis	COMB	fine	Jun	0.616	0.282	2.158	0.030
			Grass	1.010	0.436	2.289	0.022
			Temp	− 0.896	0.447	1.980	0.047

Table 4 Significant model averaged parameters of the best model for each species. The model type, scale (large or fine), estimate, standard error (SE), test value (*z*) and *p*-value are given for each parameter. Note that species where there was more than one model in the best model set (i.e. $\Delta AIC_c < 2$) are marked with *. In these cases, the model with the lowest AIC_c is presented, but competing models are shown in ESM, Table S3, along with full details for all species.

Figure 1

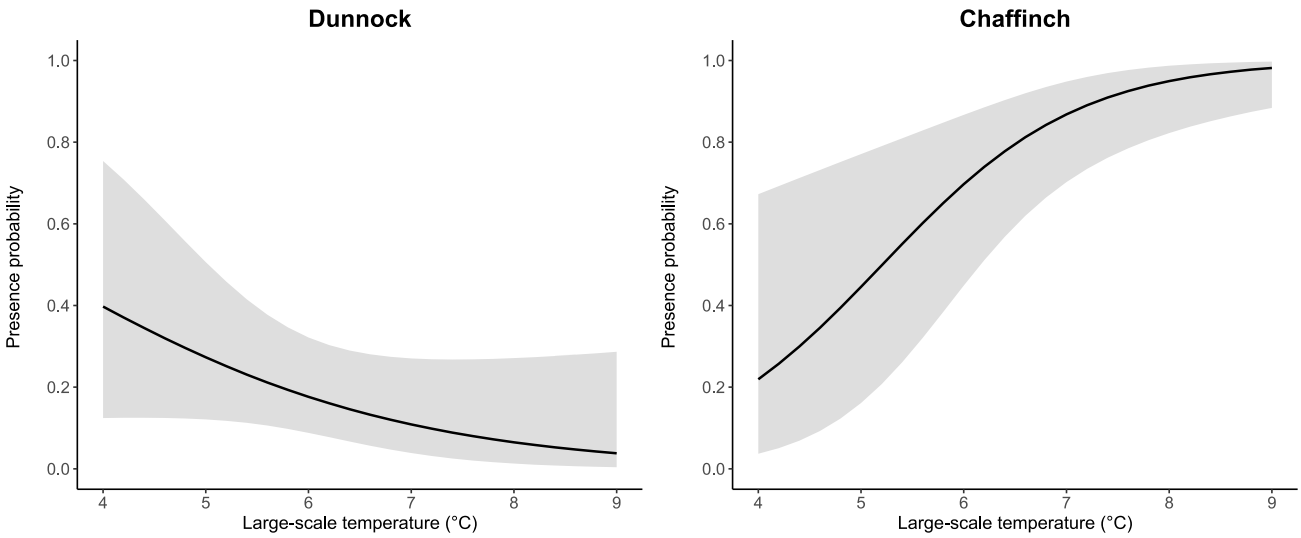


Figure 2

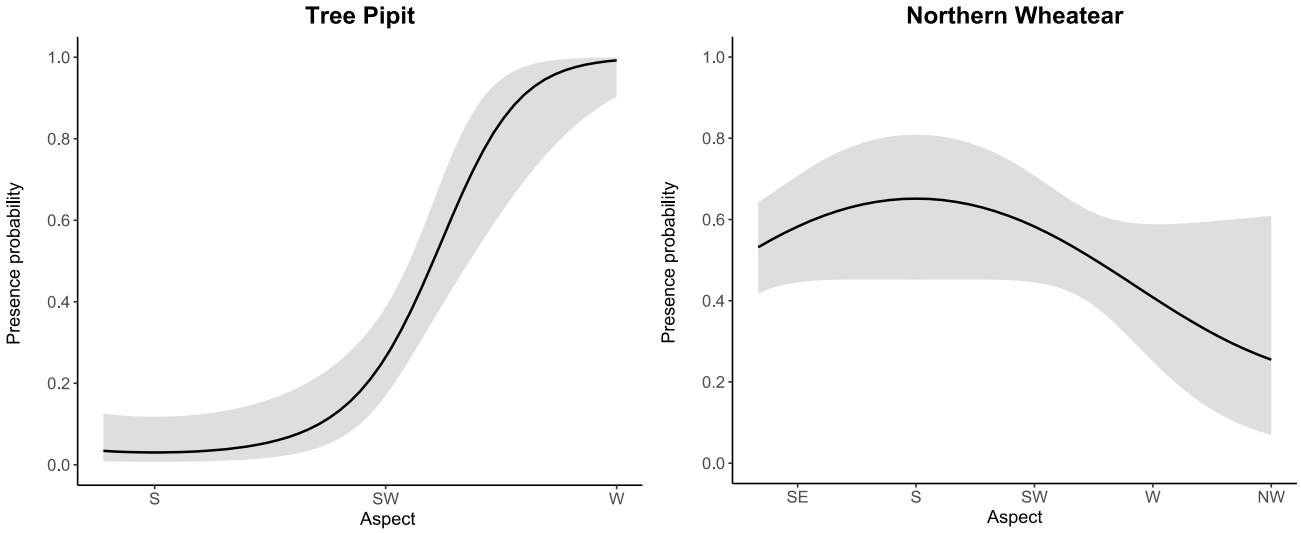
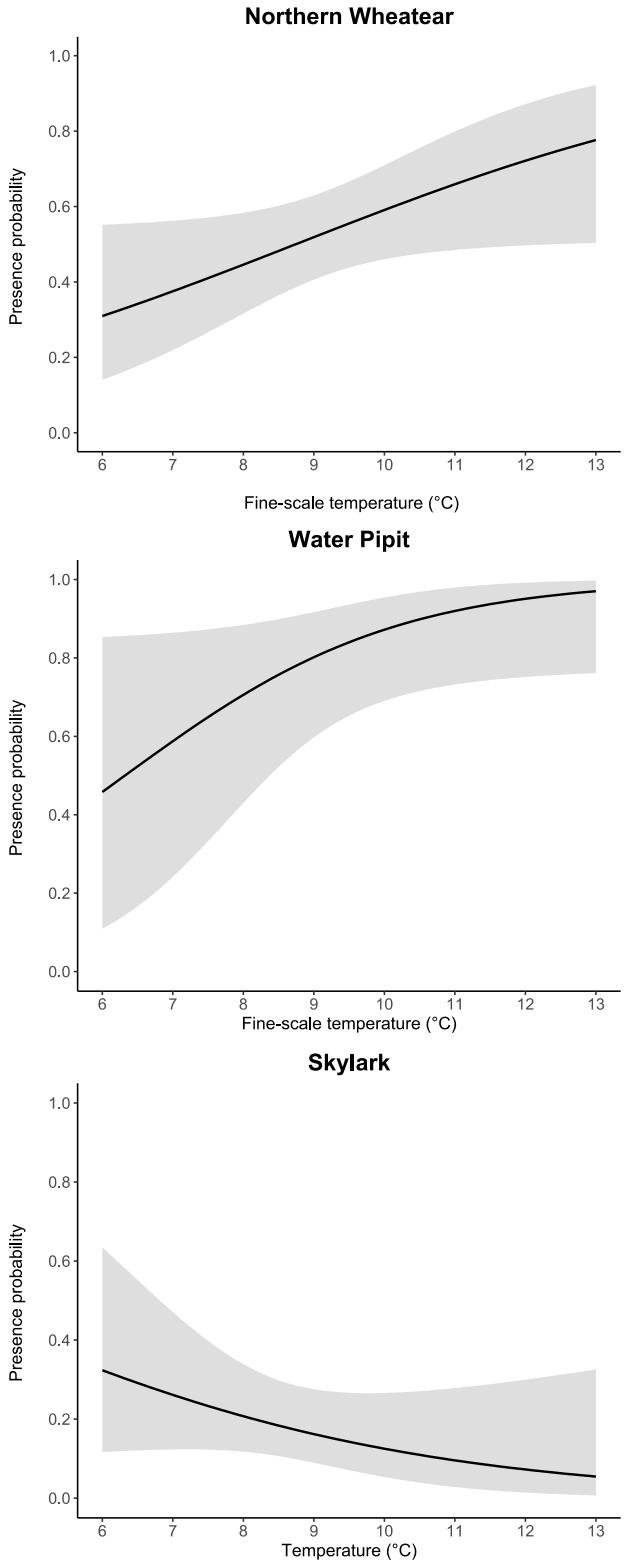


Figure 3


Northern Wheatear
Presence probability
1.0
0.8
0.6
0.4
0.2
0.0
6
7
8
9
10
11
12
13
Fine-scale temperature (°C)
Water Pipit
Presence probability
1.0
0.8
0.6
0.4
0.2
0.0
6
7
8
9
10
11
12
13
Fine-scale temperature (°C)
Skylark
Presence probability
1.0
0.8
0.6
0.4
0.2
0.0
6
7
8
9
10
11
12
13
Temperature (°C)